

**Spatial and demographic effects on
Tree Swallow nest quality and reproductive success**

by

Raleigh J. Robertson

Department of Biology, Queen's University, Kingston, Ontario K7L 3N6

and

Jason Jones

Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755

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INTRODUCTION

The reproductive success of Tree Swallows (*Tachycineta bicolor*) is affected by a number of factors. For populations nesting in natural cavities, ecological factors such as cavity volume, predation and nest usurpation are often the primary determinants of reproductive success (Rendell and Robertson 1989; Robertson and Rendell 1990; Robertson et al. 1992). For Tree Swallows occupying nest-boxes, these factors are usually not important because the researcher's use of predator guards almost eliminates predation, use of uniformly-sized boxes controls for effects of cavity volume on clutch size, and boxes with carefully designed entrance dimensions reduce nest usurpation by competitor species such as European Starlings (*Sturnus vulgaris*), Common Grackles (*Quiscalus quiscula*) and Northern Flickers (*Colaptes auratus*) (Rendell and Robertson 1991). However, in nest-box studies, other factors can influence reproductive success either directly or potentially through an effect on nest quality.

Some researchers (e.g., McCarty and Secord 1999a, b) have evaluated the potential effects of exposure to chemicals in the environment on nest quality and/or reproductive success in Tree Swallows. However, there are other variables that can have a major impact on these endpoints. Inter-nest spacing, proximity to forest edge, timing of settlement and nest-building, availability of nesting material, history of the nest-box or grid, and age of the breeding pair could all affect nest quality and/or reproductive success:

- (i) Inter-nest spacing may affect nest-building and productivity since competitive interactions become more intense when boxes are close together (Muldal et al. 1985;

Mitchell and Robertson 1996), so birds may spend more time in nest-box defense, and less time in other nesting activities.

- (ii) Proximity to edge of an open area, where shrubs or trees are close to the nest-box, may have an effect since House Wrens (*Troglodytes aedon*), which occupy shrub habitat, may interfere with Tree Swallow nesting (Rendell and Robertson 1990).
- (iii) A trend of reduced breeding success as the season progresses has been established (Stutchbury and Robertson 1988); hence, settlement date and/or the time of nest-building may also affect quality of the nest, and reproductive success.
- (iv) The type and availability of nesting material may also affect nest quality, hatching success and fledging success. The type of nesting material will likely vary from site to site, as will the availability of feathers to use as nest lining (usually waterfowl feathers). The type and number of feathers probably vary as a function of wind exposure, whether there is flowing or standing water, and the local population of waterfowl or other birds. Hence, availability of nesting materials may affect nest quality and in turn, reproductive success.
- (v) The history of an individual nest-box within a grid, or of the entire nest-box grid, may influence the quality of nests and potentially reproductive success. Since birds often return to the same box to breed, the history of a given box (i.e. old or new) may be related to the likelihood of being occupied by an experienced female or pair, which in turn may affect nest quality and/or reproductive success. Also, a grid with a long history is likely to have a stable population with many returning birds, compared

with a newly established grid, which would likely have a younger age distribution, plus more breeders new to the study site.

- (vi) Finally, female age may have an effect on nest quality and/or reproductive success, with younger, inexperienced females expected to build less substantial nests, and also to have reduced reproductive success (Stutchbury and Robertson 1988). Similarly, male age could have an effect through the male's ability to compete for nest-lining feathers, or his ability to assist with feeding nestlings.

Unless all of these factors are carefully controlled, it is difficult to pinpoint a single causal factor as being responsible for any differences between study sites in either nest quality or reproductive success. Moreover, it is not clear that nest quality affects reproductive success in Tree Swallows. Several studies that have evaluated this issue (e.g., Winkler 1993; Lombardo et al. 1995; McCarty and Secord 1999a) have reached varying results.

The purpose of this study was to determine the effects of (i) inter-nest spacing, (ii) proximity to forest edge, (iii) settlement and nest-building date, (iv) availability of nesting material, (v) history of the nest-box, and nest-box grid and (vi) female and male age, on both nest quality and reproductive success of the Tree Swallow. In addition, this study evaluated the impact of nest quality on reproductive success.

METHODS

We conducted this study using existing grids of nest-boxes, as well as adjacent, newly established grids, at the Queen's University Biological Station (QUBS), 50 km north of Kingston,

Ontario, Canada, from April through July 2001 (see map in Appendix 1). The established grids have been in place since 1984 on various hayfields owned by QUBS. Vegetation is cut annually, after completion of Tree Swallow breeding, to prevent invasion of the habitat by trees and shrubs. Adjacent hayfields were used for erecting new grids. Inverted metal cones or closed-end cylinders mounted on the support poles protected boxes from terrestrial predators (raccoons (*Procyon lotor*) and black rat snakes (*Elaphe obsoleta*)).

(i) *Inter-nest spacing* - Previously existing grids (HU, BG, SP, NB, TG) had nest-box "locations" on a 20 m x 20 m grid, with boxes in place at alternate "locations", i.e. boxes were spaced 40 m apart along rows and columns, with 28 m between boxes along the diagonal. On portions of two of these grids (BG & SP), we added boxes at the empty "locations", creating a portion of the grid with inter-nest distance of 20 m, to allow evaluation of the effects of inter-nest spacing on nest quality and on reproductive success (see maps in Appendix 2). One established grid (ST) had boxes in a regular grid at 20 m intervals.

(ii) *Proximity to edge* - Existing grids are in open fields, with edge boxes being at least 20 m from forested or shrub edges. Ten boxes were erected adjacent to these grids, at least 20 m from existing boxes but within 5 m of the forest/shrub edge to examine effects of proximity to edge on nest quality and reproductive success.

(iii) *Settlement and nest-building date* - To address the hypothesis that nest quality and reproductive success are lower in boxes with later settlement and/or later nest-building, we

visited nests every three days to record settlement of the breeding pair and the state of nest-building. Ultimately, we used first-egg date as an index of nest phenology (cf. Stutchbury and Robertson 1987a).

(iv) Availability of nesting material - In addition to the grids located in hayfields, an established grid over standing water (NES) was monitored to explore the effects of availability of nesting material on nest quality and to assess the effect of aquatic versus terrestrial habitat on reproductive success.

(v) History of the nest-box and grid - To assess the effects of the history of the nest-box grid on both nest quality and reproductive success, additional grids of nest-boxes with the same spacing as existing grids were established in an adjacent hayfield at HUB and HUC. In addition, we established new grids at SRB1 (variable spacing) and SRB2 (10m spacing). Erection of new boxes within old grids, as described above in paragraph (i) for parts of BG and SP, allowed partitioning of box history independent of grid history. The new boxes had been used previously in other studies, so they were weathered to the same extent as original boxes.

(vi) Female and male age - Adult Tree Swallows were captured for banding and aging using simple traps in nest-boxes (Stutchbury and Robertson 1986). Females were aged by plumage and classified as SY (Second Year, i.e. first-time breeders) or ASY (After Second Year, i.e. likely experienced) (Stutchbury and Robertson 1987b). Males were aged by wing length and classified

as either SY or ASY when age was known, or as AHY (After Hatch Year) when age was ambiguous (Rendell, Kempenaers and Robertson, in prep.).

Nest quality - As indicators of nest quality, we measured mass of nesting material as well as the number of feathers lining the nest (cf. McCarty and Secord 1999a). All nests were weighed on the day the first egg was laid and again on hatch-day. The number of feathers lining the cup was estimated (counted if less than 10 or if possible without disruption) on first-egg day, the day following clutch completion, and hatch-day.

Reproductive success - We used clutch size, duration of incubation, hatching success, day-10 nestling mass and fledging success as indices of reproductive success. Recruitment of offspring into the breeding population is the best measure of reproductive success, but it is nearly impossible to measure. Fledging success may be the best feasible indicator of this endpoint. However, the other measures listed above also provide useful landmarks for comparing between different populations or studies. At all nests, we recorded first-egg date, date of clutch completion, clutch size (number of eggs at clutch completion), hatch date, hatching success (number of eggs hatched, and eggs hatched/eggs laid), day-10 nestling mass, and fledging success (number nestlings fledged and nestlings fledged/nestlings hatched).

Analyses. - Statistical analyses were performed with JMP IN 4.0.2 (SAS Institute Inc. 2000). All variables that were not normally distributed (as determined by Shapiro-Wilk tests) were transformed before using in subsequent analyses. Bartlett's tests for homogeneity of variances

were performed on both the transformed and remaining untransformed variables and no significant heteroscedasticity was detected. Non-parametric tests were performed when variables were untransformable or when there were extreme sample size differences between groups. Where required, sequential Bonferroni corrections were applied to control the group-wide type-I error rates at $\alpha = 0.05$ (Rice 1989). Means \pm SE of untransformed data are presented in the tables for ease of interpretation.

RESULTS

The results of our study, analyzed by grid, are summarized in Tables 1 and 2 for measures of nest quality and reproductive success, respectively. The following sections describe the results relating to: (1) the effects of the six spatial and demographic variables evaluated on both nest quality and reproductive success; (2) inter-grid variations in measures of nest quality and reproductive success; and (3) the effects of nest quality on reproductive success.

Effects of spatial and demographic variables on nest quality and reproductive success

(i) *Inter-nest spacing* -Distance between nest-boxes in a grid, and hence nesting density, was related to several aspects of nest quality. The number of occupied boxes within 20 meters was negatively correlated with nest mass at first egg (Spearman's $Rho = -0.25$, $P=0.006$) and nest mass at hatch ($Rho = -0.26$, $P=0.005$). That is, with more close neighbors, pairs built nests of lower mass. At greater inter-nest distance, neither of these relationships held.

Some parameters of breeding phenology and indices of reproductive success were significantly related to inter-nest spacing. The number of occupied boxes within 20 meters was negatively correlated with incubation period ($Rho = -0.29$, $P=0.002$); that is, incubation periods were shorter in areas of higher nest-box density. Consistent with this negative effect of too close neighbors, the number of fledglings ($Rho = -0.27$, $P=0.004$) was negatively correlated with number of boxes within 20 meters.

(ii) *Proximity to edge* - Some aspects of breeding phenology (i.e., first-egg date) and some indices of reproductive success were correlated with the proximity of an occupied nest-box to shrub or woodland vegetation. Nests further from edge had earlier first egg dates ($r=-0.23$, $P=0.003$) and larger clutch size ($r=0.36$, $P=0.0001$), as well as a longer incubation period ($r=0.36$, $P=0.0001$). However, there was no significant correlation between distance to edge and brood size, day-10 nestling mass, or number fledged.

SY females settled closer to edge (24.6 ± 7.1 m) than did ASY females (35.4 ± 2.7 m) ($t = 2.09$, $df = 88$, $P=0.04$), so the relationship between edge and reproductive parameters, especially clutch size, may occur because of age-dependent settling patterns, rather than an impact of edge per se.

(iii) *Settlement and nest building date* - Breeding phenology, measured by first-egg date, was not correlated with either the mass of the nest or the number of feathers. Phenology was, however, related to reproductive success. First-egg date was negatively correlated with both mean

nestling mass on day-10 ($r = -0.20$, $P = 0.04$), and with number of fledglings ($r = -0.28$, $P = 0.003$), meaning that earlier nests generally had higher reproductive success.

(iv) *Availability of nesting material* - There were no clear patterns relating either nest quality or reproductive success to availability of nesting material associated with aquatic versus terrestrial habitats. Although we did not directly measure availability of nesting material in relation to habitat, NES, the grid over water, did not stand out from the others in terms of either nest mass or feather number (Table 1), nor in terms of reproductive success (Table 2).

(v) *History of the grid and nest-box* - Certain aspects of nest quality appear to be related to grid and nest-box history. Contrary to expectations, birds in new grids had more feathers in their nests at last egg (new = 14.2 ± 2.3 , old = 7.2 ± 0.5 , $U = 2.93$, $P = 0.003$), than those in older grids. However, by hatch, there were no significant differences in number of feathers in relation to grid age, nor were there differences in nest mass.

Reproductive success was also related to grid history. Birds in newly established grids nested later (First egg date (1 May = day 1) new = 22.4 ± 3.4 , old = 12.2 ± 0.6 ; $U = 3.34$, $P = 0.0008$), had shorter incubation periods (new = 17.8 ± 0.1 , old = 19.0 ± 0.3 , $U = 3.63$, $P = 0.0003$), had smaller clutches (new = 4.5 ± 0.2 , old = 5.6 ± 0.1 , $U = 3.96$, $P < 0.0001$) and smaller brood sizes (new = 4.0 ± 0.3 , old = 4.8 ± 0.2 , $U = 2.71$, $P = 0.007$) than those nesting in previously established (old) grids.

When comparing nesting parameters for newly erected boxes in previously established grids with original boxes in those same grids, it becomes apparent that the history of the

individual box itself can also have an effect on nest quality and reproduction. New boxes contained nests with lower mean mass at the time of the first egg (new = 25.7 ± 1.2 , original 31.8 ± 1.6 , $U = 2.12$, $P = 0.03$) and at hatch (new = 26.7 ± 1.2 , original = 32.4 ± 1.3 , $U = 2.41$, $P = 0.02$) than original boxes, although there were no differences in number of feathers at any stage.

The history of the individual box was also related to breeding phenology and indices of reproductive success. Pairs occupying new boxes had later clutch initiation (new = 18.5 ± 2.2 , original = 11.6 ± 0.4 , $U = 2.67$, $P = 0.008$), shorter incubation periods (new 18.3 ± 0.1 , old = 19.1 ± 0.3 , $U = 3.60$, $P = 0.0003$), smaller clutch size (new = 4.9 ± 0.2 , original = 5.7 ± 0.09 , $U = 4.26$, $P < 0.0001$), smaller brood size (new = 4.2 ± 0.3 , original = 4.9 ± 0.02 , $U = 2.77$, $P = 0.006$), lower day-10 nestling mass (new = 18.3 ± 0.6 , original = 19.7 ± 0.2 , $U = 2.39$, $P = 0.02$) and fledged fewer young per nest (new = 2.9 ± 0.4 , original = 4.2 ± 0.2 , $U = 2.79$, $P = 0.005$) than did pairs in original boxes.

(vi) *Effects of female and male age* - Although we expected measures of nest quality to be related to female age, comparison of SY versus ASY females revealed no effects of female age on either nest mass (SY = 38.5 ± 8.3 g, ASY = 29.3 ± 1.1 g; Mann-Whitney $U = 0.75$, $P = 0.46$) or number of feathers in the nest lining (SY = 3.4 ± 1.6 , ASY = 3.0 ± 0.4 ; $U = 0.29$, $P = 0.78$). However, reproductive output was related to female age as expected. ASY females had earlier first egg dates ($U = 2.04$, $P = 0.004$), laid larger clutches (ASY = 5.7 ± 0.1 , $n=78$; SY = 4.6 ± 0.3 , $n=12$; $U = 3.61$, $P = 0.0003$), had larger brood size (ASY = 5.1 ± 0.1 , SY = 4.3 ± 0.4 ; $U = 2.38$, $P = 0.017$), and fledged more young (ASY = 4.3 ± 0.2 , SY = 3.1 ± 0.6 , $n=11$; $U = 2.44$, $P = 0.015$) than SY females. Interestingly, ASY females also had longer incubation periods ($U = 2.37$, $P = 0.02$), which might

simply be a function of cooler ambient temperatures early in the season when ASY females start laying.

Male age was related to number of feathers at the time the first egg was laid (Wilcoxon $Z=12.0$, $P=0.003$, $SY=2.6 \pm 0.7$, $AHY=2.6 \pm 0.6$, $ASY=5.7 \pm 1.0$), but it was not related to number of feathers at either clutch completion or hatch. Male age was not related to number of young fledged, or to other indices of reproductive success.

Inter-grid variation in nest quality and reproductive success

We found significant variation among grids in measures of both nest quality and reproductive success. Some of this variation may be due to the variables examined above, or to other grid-related aspects of habitat (e.g. distance to good foraging areas), social interactions (e.g. size of the local breeding population) or other unidentified variables.

Table 1 shows the extent of variation among study grids in our measures of nest quality. Differences were especially marked for number of feathers at first egg and at clutch completion (last egg). Interestingly, by the time of hatching, the number of feathers lining the nest was not different among the 11 grids of nest boxes. Nest mass at first egg and at hatch also showed significant variation among grids, with NB (terrestrial) and NES (aquatic) having relatively high mass, ST and TG (both terrestrial) having low mass, and the other 7 grids being intermediate. It is noteworthy that neither difference in nest mass nor feather number followed obvious differences in habitat type, i.e. terrestrial versus aquatic, nor potential differences in availability of nesting materials.

We also found significant variation among grids in several measures of reproductive success, as shown in Table 2. The proportion of boxes occupied (completed clutch), the proportion of completed clutches that fledged and the proportion of hatching broods that fledged, all exhibited significant grid-to-grid variation. Also, clutch size, day-10 nestling mass, number fledged per complete clutch and number fledged per brood hatched varied significantly among grids. However, not all indices of reproductive success showed significant variation among grids. The proportion of complete clutches that hatched at least some young, the number of nestlings per clutch laid, the number of nestlings per brood, and the number fledged per successful nest showed no significant differences among the 11 grids.

Effects of nest quality on reproductive success

There was little evidence that nest quality affected reproductive success. While nest quality was related to some possible indicators of success, namely duration of the nestling period and nestling growth, nest quality was not related to actual reproductive output measured by either number or percentage of nestlings fledged.

Incubation - Nest quality had no effect on the length of the incubation period. Neither number of feathers at last egg ($r=-0.002$, $F=0.0004$, $P=0.98$) nor nest mass at first egg ($r=-0.14$, $F=0.21$, $P=0.65$) was related to the length of the incubation period.

Hatch - Neither the number of feathers at last egg nor number of feathers at hatch was significantly correlated with hatching success (# hatched/clutch size) (Spearman Rho = 0.0041,

$P=0.96$, and $Rho = -0.052$, $P=0.58$ respectively). Nest mass at hatch was also unrelated to hatching success ($Rho = -0.0554$, $P=0.56$).

Growth & nestling period - We did see some indication of an effect of feather number on nestling growth. Although the numbers of feathers at first egg ($r=0.34$, $F=0.55$, $P=0.46$) and at clutch completion ($r=0.21$, $F=1.32$, $P=0.25$) were not significantly related to nestling mass at day-10, the number of feathers at hatch was positively related to day-10 nestling mass ($r=0.06$, $F=7.86$, $P=0.006$).

Nest mass did not appear to influence nestling growth. Neither nest mass at first egg ($r=0.13$, $F=0.06$, $P=0.81$) nor at hatch ($r=0.61$, $F=0.97$, $P=0.33$) was significantly related to day-10 nestling mass.

We did find that young fledged sooner from heavier, well-feathered nests. The number of feathers at hatch ($r=-0.04$, $F=4.61$, $P=0.035$) and nest mass at hatch ($r=-1.20$, $F=6.39$, $P=0.013$) were both negatively related to the length of the nestling period.

Fledging - Reproductive output was not significantly related to any of our measures of nest quality. Specifically, the number of feathers at first egg ($r=0.29$, $F=0.41$, $p=0.52$), the number of feathers at clutch completion ($r=0.20$, $F=1.15$, $P=0.29$), and the number of feathers at hatch ($r=0.04$, $F=3.36$, $P=0.07$) were all unrelated to the number fledged per nest. Similarly, fledging success measured as percent fledged ($\# \text{ fledged} / \# \text{ hatched}$) was not correlated with number of feathers at hatch ($Rho = 0.2012$, $P=0.02$; not significant after Bonferroni correction).

Nest mass also had no direct effect on fledging success. Neither nest mass at first egg nor at hatch had an effect on the number of fledglings produced ($r=0.47$, $R=0.69$, $P=0.41$ and $r=0.64$, $F=0.93$, $P=0.34$, respectively). Likewise, nest mass at hatch had no effect on the percentage of nestlings that fledged ($Rho = 0.0069$, $P=0.94$).

We did find that nestling mass at day-10 was positively related to both number fledged ($r=0.18$, $F=4.85$, $P=0.03$) and proportion fledged per brood ($r=0.04$, $F=8.75$, $P=0.004$). As noted above, 10-day nestling mass was also positively correlated with feather number at hatch. However, since we did not find a direct correlation of feather number with fledging success, there are likely other contributors to day-10 nestling mass and hence fledging success that have nothing to do with feather number.

DISCUSSION

Our study shows that many aspects of the study grid can have a significant influence on measures of nest quality, such as nest mass and feather number, and on reproductive success. Nests at higher densities had lower nest mass at both first egg and hatch, later clutch initiation, shorter incubation periods, lower mean nestling mass at day-10, and they also produced fewer fledglings than nests with fewer or no nests within 20 m. These findings provide an adaptive explanation for earlier studies that showed within distances of about 20 m, Tree Swallows preferred to space their nests as far as possible from nesting conspecifics (Muldal et al. 1985). This and earlier studies indicate that if meaningful comparisons are to be made between Tree

Swallows breeding in different habitats, or exposed to different levels of chemicals in the environment, it is critical to provide nest boxes that are sufficiently far apart to minimize interference from neighbors, and also to achieve a level of consistency in inter-box spacing so that comparisons are meaningful.

Another aspect of nest spacing that must be considered is the location of a nest with respect to surrounding trees and shrubs. In our study, nest phenology and reproductive ecology were correlated with distance to the edge. Nests close to forest edge were less substantial in terms of mass, and clutches were smaller and were initiated later than nests more distant from the edge.

Some of these effects of spatial ecology on nest quality and reproductive success could be driven by female age. Although we did not find female age to be significantly correlated with either nest mass or feather number, we did find, as have previous studies (e.g. Stutchbury and Robertson 1988), that older females have greater reproductive success than second-year females. In terms of potential edge effects, second-year females settled closer to the edge than did after-second-year females. Since nests near forest edge often suffer interference from House Wrens or from snakes and other terrestrial predators, there appears to be selection against nesting near the forest edge (Rendell and Robertson 1990). Even if there were no age-related settling pattern, it is likely that experienced females would occupy the preferred nest sites away from edge, while less experienced or subordinate females would occupy nest-boxes near forest edge. Given this effect, it is critical that when making comparisons between different studies, the configuration of nest-boxes relative to forest edge is considered as a possible confounding variable. Consequently, it is important to control for both configuration of nest-boxes and age

of female in any situation where there may be density effects or where the age distribution might differ between study populations.

Tree Swallows are known to experience a decline in reproductive success as the season advances (Stutchbury and Robertson 1988). Part of this seasonal decline may be related to younger females nesting later, but a decline with time of the breeding season occurs even within female age classes. Results of our current study are consistent with previous work. This seasonal decline in reproductive output means that factors that can affect breeding phenology must be also considered when making comparisons between different habitats or study sites.

Although we found no differences in nest quality due to potential differences in availability of nesting materials when comparing grids in aquatic and terrestrial habitat, this is perhaps not surprising. Most of our terrestrial grids are near beaver ponds, which apparently have an ample supply of waterfowl feathers. The absence of habitat effects on reproductive success may also be due to the heterogeneous habitat in the vicinity of our study grids, with numerous ponds and hence good foraging areas nearby producing an abundance of emergent aquatic insects. That is not to say that breeding habitat can be ignored as a factor when comparing different studies. In other situations, if nest-boxes were located in an area where feathers or other nesting material were in short supply, this factor could potentially affect nest quality and/or reproductive success, independently of other environmental variables.

Our study also showed that grid and nest-box histories were correlated with both nest structure and reproductive success. For unknown reasons, nests in new grids had more feathers during early stages of nesting than those in established grids. However, by the time of hatch, the differences had disappeared. Established grids had earlier mean first egg dates, longer

incubation periods, larger mean clutch size, brood size and greater fledging success than did newly established grids. Clearly, the history of the grid, and hence the local breeding population can have an important influence on reproductive success.

Indeed, the history of the grids may have been largely responsible for the differences in reproductive success of Tree Swallows in 1994 and 1995 reported by McCarty and Secord (1999b) for sites along the Hudson River. Since their grids were first established in 1994, the grid during that year, which had lower reproductive success, was newly established, compared to 1995, by which time it was a relatively well established grid. Again, if comparisons between Tree Swallow populations in different areas, or in different years, are to be valid, the history of the populations must be comparable.

The history of the nest-box within the grid can also affect reproduction. We found that newly erected boxes in previously established grids had later laying, shorter incubation periods, smaller clutches and broods and produced fewer fledglings than boxes which were part of the original grid. Some of these relationships may be due to younger or inexperienced females settling in newly established grids or boxes. For example, Blancher and McNicol (1988) found that older boxes attracted a significantly greater proportion of adult females than newly erected boxes did. Other factors related to nest-box history may also affect nesting behavior and success. It is likely that aggressive interactions are more common at higher density (Mitchell and Robertson 1996), and perhaps in newly established grids or boxes, resulting in a trade-off between defending the nest site and nest-building or caring for the brood. Whatever the cause of the relationships, it is necessary to control for all variables that can affect reproductive

success when analyzing for potential effects of any particular environmental variable on reproductive success of Tree Swallows.

Inter-grid variation

McCarty and Secord (1999a) examined nest quality in Tree Swallows in a number of grids with differing levels of chemical exposure. They found significant variation in nest quality among grids that coincided with varying levels of chemical exposures and suggested that food chain exposures to the birds led to abnormal nest-building behaviour. In our study, Tree Swallows occupying all eleven grids were presumably exposed to similarly low levels of environmental contamination, and individuals nesting in these grids would have occupied similar winter habitat and followed the same migration pathways. Consequently, there is no reason to believe that there are differences in exposure to chemicals in the environment among the resident birds occupying the grids of this study. Nevertheless, Tree Swallows nesting in the 11 grids of our study showed significant variation among grids, both in measures of nest quality and in reproductive success. Indeed, the mean clutch size varied from 4.0 to 5.93 eggs across the 11 grids in our study, compared to a range of 5.2 to 6.0 reported by McCarty and Secord (1999). Likewise, the mean nestling mass on day 10 in our 11 grids ranged from 16.10 to 23.30 g, whereas McCarty and Secord (1999) reported that the mean nestling mass on day 10 ranged from 19.1 to 21.8 g. Our analysis reveals that the variation is influenced by inter-nest spacing, the configuration of the grid relative to surrounding forest, breeding phenology, history of the nest-box and the grid, and female age distribution, as discussed above, as well as perhaps other unidentified variables. Clearly, a number of factors unrelated to chemicals in the environment

can affect both nest quality and reproductive success. Thus, to determine whether chemicals in the environment affect reproduction, it is first necessary to control for these other factors.

Effect of nest quality on reproductive success

This study revealed little evidence that measures of nest quality, namely number of feathers lining the nest cup and nest mass, affect reproductive success. Indeed, we found no direct effects of these nest attributes on either the length of the incubation period or on reproductive success. However, we did find that nestlings in well-feathered nests grew faster and required a shorter time in the nest prior to fledging.

Studies by Winkler (1993), Lombardo et al. (1995), McCarty and Secord (1999a) and this one, that examine the effects of nest quality on reproductive success, have produced mixed results (Table 3). Two of three studies that measured incubation time found that it is slightly shorter in well-feathered nests. All four studies found that a well-feathered nest was correlated with faster nestling growth (nestling mass on day 10 or day 12). Three of four studies found well-feathered nests had earlier fledging than poorly feathered nests. Most importantly, however, only one of the four studies found a relationship between number of feathers at hatch and the number of young fledged from the nest, and that was from an experimental study (Lombardo et al. 1995) in which all feathers were removed from some nests. Consequently, there is little evidence that the normal range of feather lining found in nests has an impact on reproductive success.

Nest mass is similarly variable in its effect on reproduction. Neither McCarty and Secord (1999a) nor this study found a significant relationship between nest mass and nestling growth

or fledging success. Lombardo (1994) did find some aspects of nest mass correlated with hatching success in part of the season, but not later, when nestling hyperthermia was more pronounced in more massive nests. Taken together, it seems that while feather lining and nest mass may play a role in determining nesting success in some cases, the effect is quite variable. Clearly, we cannot assume that nest mass and feather number are meaningful measures of nest quality, nor predictors of reproductive success.

Summary

This study demonstrates that a number of variables related to spatial ecology and anthropogenic influences such as grid or nest-box history can influence both the quality of the nest and reproductive success of Tree Swallows (summarized in Table 4). Consequently, if meaningful conclusions are to be drawn about the effects of factors such as chemical exposure on Tree Swallow nesting behaviour and reproductive success, it is important that these other variables be carefully controlled. Without consideration of the confounding effects of inter-nest spacing, distance to edge, breeding phenology, habitat, history of the nest-box and the grid, and female age, it is inappropriate to try to claim causal relationships between exposures to chemicals in the environment and either nest quality or reproductive effects in Tree Swallows. Additionally, our study indicates little or no effect of nest quality on reproductive success in this species.

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Table 1. Quality of Tree Swallow nests measured by nest mass and number of feathers lining the nest cup in 11 study grids in eastern Ontario. Treatment indicates grid history, inter-box spacing (along rows and columns), and presence of edge boxes. Values are mean \pm SE of untransformed variables, with n in parentheses; F values are from ANOVAs testing the effect of grid on nest quality. Within rows, grids that share a letter in the superscript do not differ significantly based on Tukey-Kramer HSD post-hoc tests. Bold-faced P -values are significant following sequential Bonferroni correction for multiple comparisons.

Grid	BG	HU	HUB	HUC	NB	NES	SP	SRB1	SRB2	ST	TG	F	P
Treatment	"new" boxes in existing grid, 1/2 grid at 20 m & 1/2 at 40 m + edge boxes	existing grid at 40 m	new grid at 40 m	new grid at 20 m	existing grid at 40 m + edge boxes	over water 20 to 40 m	1/2 grid at 20 m 1/2 at 40 m + edge boxes	new grid, variable spacing	new grid at 10 m	existing grid at 21 m	existing grid at 40 m		
First Egg Nest Mass (g)	26.5 \pm 1.4 ^{ab} (30)	29.5 \pm 2.3 ^{ab} (17)	28.1 \pm 0.7 ^{ab} (2)	27.4 \pm 3.6 ^{ab} (4)	34.0 \pm 3.3 ^a (10)	40.1 \pm 3.7 ^a (30)	28.7 \pm 1.8 ^{ab} (7)	25.5 \pm 2.3 ^{ab} (6)	22.4 (1)	18.7 \pm 2.0 ^b (7)	18.5 \pm 1.5 ^b (5)	5.62	<0.0001
Hatch Nest Mass (g)	26.9 \pm 1.3 ^{ab} (28)	31.2 \pm 2.2 ^{ab} (17)	29.1 \pm 1.3 ^{ab} (2)	27.5 \pm 4.2 ^{ab} (4)	35.7 \pm 2.6 ^a (9)	38.6 \pm 2.5 ^a (30)	29.8 \pm 2.6 ^{ab} (6)	26.5 \pm 2.0 ^{ab} (6)	27.0 (1)	21.1 \pm 0.6 ^b (6)	21.0 \pm 1.7 ^b (5)	5.51	< 0.0001
First Egg Feathers	1.7 \pm 0.7 ^{a,b,c} (30)	3.9 \pm 1.0 ^{bd} (17)	14.5 \pm 2.5 ^c (2)	4.3 \pm 1.6 ^{a,b,c,e} (4)	1.4 \pm 0.6 ^{a,b,c} (10)	5.1 \pm 0.6 ^{d,e} (30)	0.0 \pm 0.0 ^c (7)	3.2 \pm 1.0 ^{a,b,c,e} (6)	4.0 (1)	3.9 \pm 2.1 ^{a,b,c,d} (7)	0.2 \pm 0.2 ^{a,b,c,d} (5)	7.38	< 0.0001
Last Egg Feathers	5.4 \pm 0.8 ^a (30)	10.0 \pm 0.8 ^b (17)	20.0 \pm 4.0 ^b (2)	14.0 \pm 4.5 ^b (4)	3.9 \pm 1.4 ^a (10)	10.5 \pm 0.8 ^a (30)	2.0 \pm 1.2 ^a (7)	13.0 \pm 3.8 ^b (6)	10.0 (1)	6.0 \pm 2.2 ^{ab} (6)	4.6 \pm 1.4 ^{ab} (5)	9.21	<0.0001
Hatch Feathers	19.3 \pm 1.6 (28)	27.4 \pm 2.3 (17)	23.0 \pm 0.0 (2)	21.3 \pm 3.6 (4)	17.0 \pm 2.3 (9)	23.3 \pm 1.6 (30)	14.0 \pm 4.2 (6)	23.7 \pm 6.1 (6)	32.0 (1)	22.0 \pm 6.1 (6)	17.2 \pm 2.7 (5)	1.89	0.06

Table 2. Tree Swallow reproductive success, analyzed by grid. For first egg date, May 1 = day 1. Statistics as in Table 1.

Grid	BG	HU	HUB	HUC	NB	NES	SP	SRB1	SRB2	ST	TG	Stats
Treatment	"new" boxes in existing grid, 1/2 grid at 20 m & 1/2 at 40 m + edge boxes	existing grid at 40 m	new grid at 40 m	new grid at 20 m	existing grid at 40 m + edge boxes	over water 20 to 40 m	1/2 grid at 20 m 1/2 at 40 m + edge boxes	new grid, variable spacing	new grid at 10 m	existing grid at 21 m	existing grid at 40 m	
# boxes	53	24	8	15	17	35	19	25	9	12	10	
First egg date Mean \pm 1 SE	13 \pm 1	10 \pm 1	25 \pm 13	23 \pm 8	13 \pm 2	11 \pm 1	17 \pm 4	22 \pm 5	16 \pm 1	14 \pm 3	13 \pm 1	
# clutches completed	30	17	2	4	10	30	7	6	1	7	5	
% boxes with complete clutch	56.60%	70.83%	25.00%	26.67%	58.82%	85.71%	36.84%	24.00%	11.11%	58.33%	50.00%	$\chi^2=42.16$ df=10 P<0.001
clutch size (Mean \pm SE)	5.43 ^{ab} \pm 0.11	5.76 ^a \pm 0.16	4.00 ^{ab} \pm 0.00	5.00 ^{ab} \pm 0.41	5.30 ^{ab} \pm 0.30	5.93 ^{ab} \pm 0.13	5.29 ^{ab} \pm 0.18	4.33 ^b \pm 0.42	5.00 \pm 0.75	5.00 ^{ab} \pm 0.75	5.60 ^{ab} \pm 0.25	F=3.72 df=9 P=0.0004
# broods hatched	28	17	2	4	9	30	6	6	1	6	5	
% clutches hatched	93.33%	100.00%	100.00%	100.00%	90.00%	100.00%	85.71%	100.00%	100.00%	85.71%	100.00%	$\chi^2=7.66$ df=10 P=0.98
nestlings/brood (Mean \pm SE)	4.79 \pm 0.24	5.06 \pm 0.25	4.00 \pm 0.00	4.25 \pm 0.63	5.11 \pm 0.31	5.17 \pm 0.21	5.16 \pm 0.17	4.17 \pm 0.54	2.00	5.17 \pm 0.40	5.24 \pm 0.26	F=1.05 df=9 P=0.41
nestlings/clutch laid (Mean \pm SE)	4.47 \pm 0.31	5.06 \pm 0.25	4.00 \pm 0.00	4.25 \pm 0.63	4.60 \pm 0.58	5.17 \pm 0.21	4.43 \pm 0.75	4.17 \pm 0.54	2.00	4.43 \pm 0.81	5.24 \pm 0.26	F=0.86 df=9 P=0.56
D10 mass (Mean \pm SE)	18.90 ^{ab} \pm 0.36	20.57 ^a \pm 0.50	-	16.10 ^b \pm 2.93	20.12 ^{ab} \pm 0.69	19.78 ^{ab} \pm 0.33	18.46 ^{ab} \pm 1.09	18.85 ^{ab} \pm 1.10	23.30	20.30 ^{ab} \pm 0.72	16.87 ^{ab} \pm 1.31	F=3.13 df=8 P=0.0035
# broods fledged	21	13	0	2	7	30	5	4	1	6	5	
# fledged per successful nest (Mean \pm SE)	4.29 \pm 0.35	4.86 \pm 0.47	0	5.00 \pm 1.41	5.00 \pm 0.38	4.93 \pm 0.24	3.40 \pm 0.51	4.50 \pm 0.50	2.00	4.67 \pm 0.49	4.80 \pm 0.37	F=0.22 df=9 P=0.22
% hatching broods fledged ≥ 1	75.00%	76.47%	0.00%	50.00%	77.78%	100.00%	83.33%	66.67%	100.00%	100.00%	100.00%	$\chi^2=23.92$ df=10 P<0.01

# fledged per brood hatched (Mean \pm SE)	3.21 ^{ab} \pm 0.44	4.00 ^{ab} \pm 0.66	0 ^b	2.50 ^{ab} \pm 1.50	3.89 ^{ab} \pm 0.79	4.93 ^a \pm 0.24	2.83 ^{ab} \pm 0.70	3.00 ^{ab} \pm 1.00	2.00	4.00 ^{ab} \pm 0.79	4.00 ^{ab} \pm 0.86	F=2.56 df=9 P=0.011
% completed clutches fledged \geq 1	70.00%	76.47%	0.00%	50.00%	70.00%	100.00%	71.43%	66.67%	100.00%	85.71%	100.00%	Xi ² =22.12 df=10 P=0.03
# fledged per complete clutch (Mean \pm SE)	3.00 ^b \pm 0.44	4.00 ^{ab} \pm 0.60	0 ^{ab}	2.50 ^{ab} \pm 1.50	3.50 ^{ab} \pm 0.81	4.93 ^a \pm 0.24	2.43 ^{ab} \pm 0.72	3.00 ^{ab} \pm 1.00	2.00	4.00 ^{ab} \pm 0.79	4.00 ^{ab} \pm 0.86	F=2.66 df=9 P=0.008

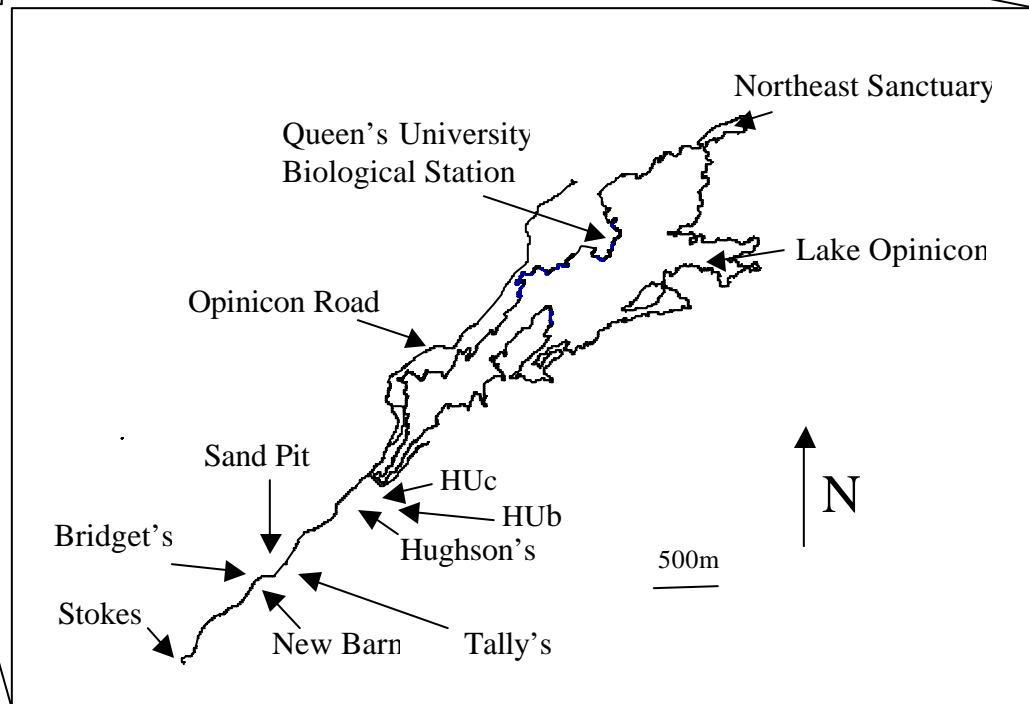
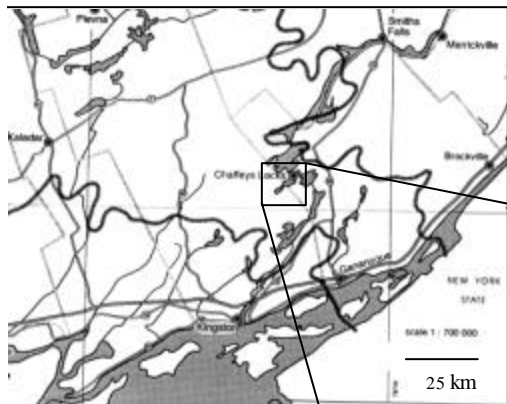
Table 3. Effects of feather lining on reproductive success: comparison of four studies.

Nest attribute & indicator of reproductive success	Winkler (1993)	McCarty and Secord (1999a)	Lombardo et al. (1995)	This study
Feathers at start of incubation (last egg) & length of incubation	not measured	negative relation (Fig 2), i.e. fewer feathers, longer incubation (significant, but weak relationship)	nests with feathers had significantly shorter (12.40d) incubation than those without feathers (13.21d)	no correlation ($r=-0.002$, $F=0.0004$, $P=0.98$)
Feathers at hatch & nestling mass on day 10 or day 12	experimental removal of feathers led to lower d12 mass (Fig3)	nestlings in well feathered nest heavier on d10 (Fig 3), but not significantly so after outlier is removed	feathered nests had significantly heavier nestlings at d12	$r=0.06$, $F=7.86$, $P=0.006$, i.e. positive effect of feathers on growth to d10
Feathers at hatch & length of nestling period	nests with more feathers fledged at younger age (1 in 3 years) (p31), yet he did not measure time to fledge in his follow-up experiment (??)	no significant correlation	nestling period shorter in nests with feathers than those with none, but not significantly so.	negative correlation i.e. more feathers, earlier fledge ($r=-0.04$, $F=4.61$, $P=0.035$)
Feathers at 1st egg & number fledged	not measured	positive correlation ($R^2=0.05$, $P=0.037$, Fig4) - (effect must be on number hatched, but not tested)	not measured	no effect ($r=0.29$, $F=0.41$, $P=0.52$)
Feathers at hatch & number fledged	experimental removal had no effect on number fledged	no effect of number of feathers at hatch	experimental removal of feathers - nests with no feathers fledged fewer young	no effect of feathers at hatch and number fledged. ($r=0.04$, $F=3.36$, $P=0.07$)

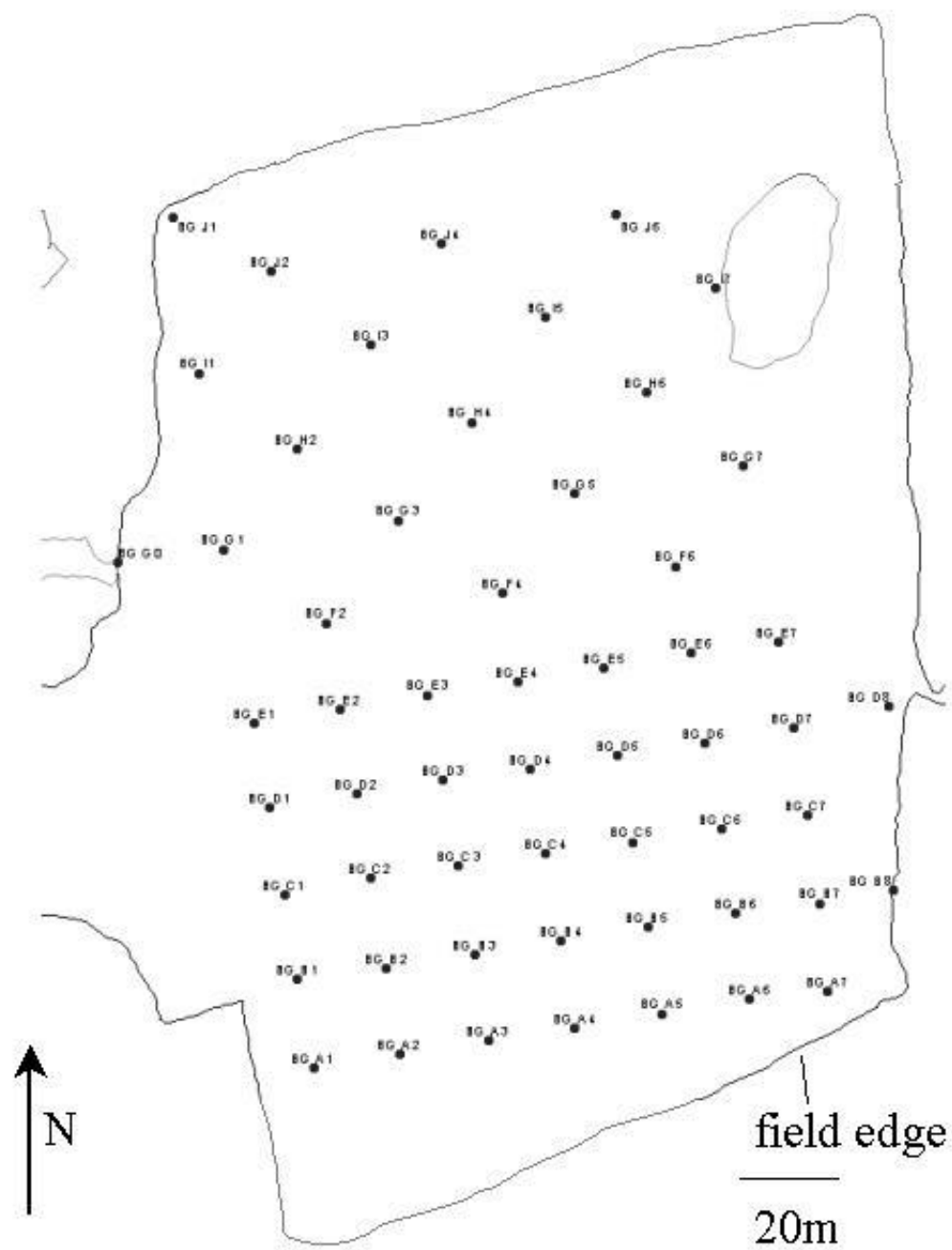
Table 4. Summary of variables studied and demonstrated significant effects on Tree Swallow nest quality and reproductive success.

Variable	Effect on	
	Nest Quality	Reproductive Success
Nest Density	yes	yes
Distance to edge	yes	yes
Female age	no	yes
Phenology (1st egg date)	no	yes
Habitat (source/availability of nest material)	no	no
History of grid	yes	yes
History of nest-box	yes	yes
Nest quality	not applicable	no

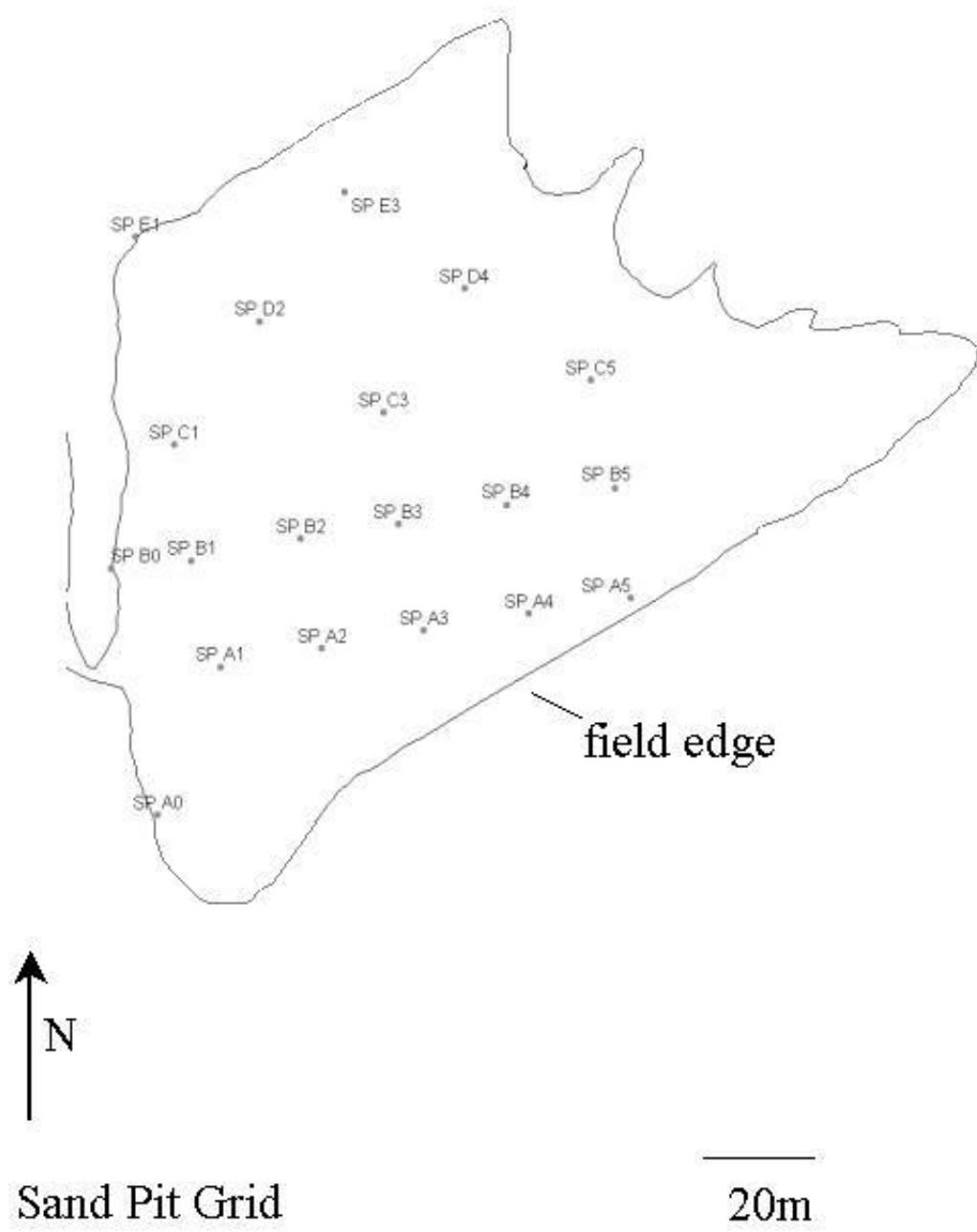
Appendix 1. Regional map showing Queen's University Biological Station at Chaffey's Lock, on Lake Opinicon, in relation to Kingston and Smiths Falls, Ontario, Canada. Study grids include Bridget's Grid (BG), Sand Pit (SP), Stokes (ST), HU (Hughson's), Hughson's B (HUB), Hughson's C (HUC), NB (New Barn), Tally's Grid (TG), SRB1, SRB2, and the Northeast Sanctuary (NES).

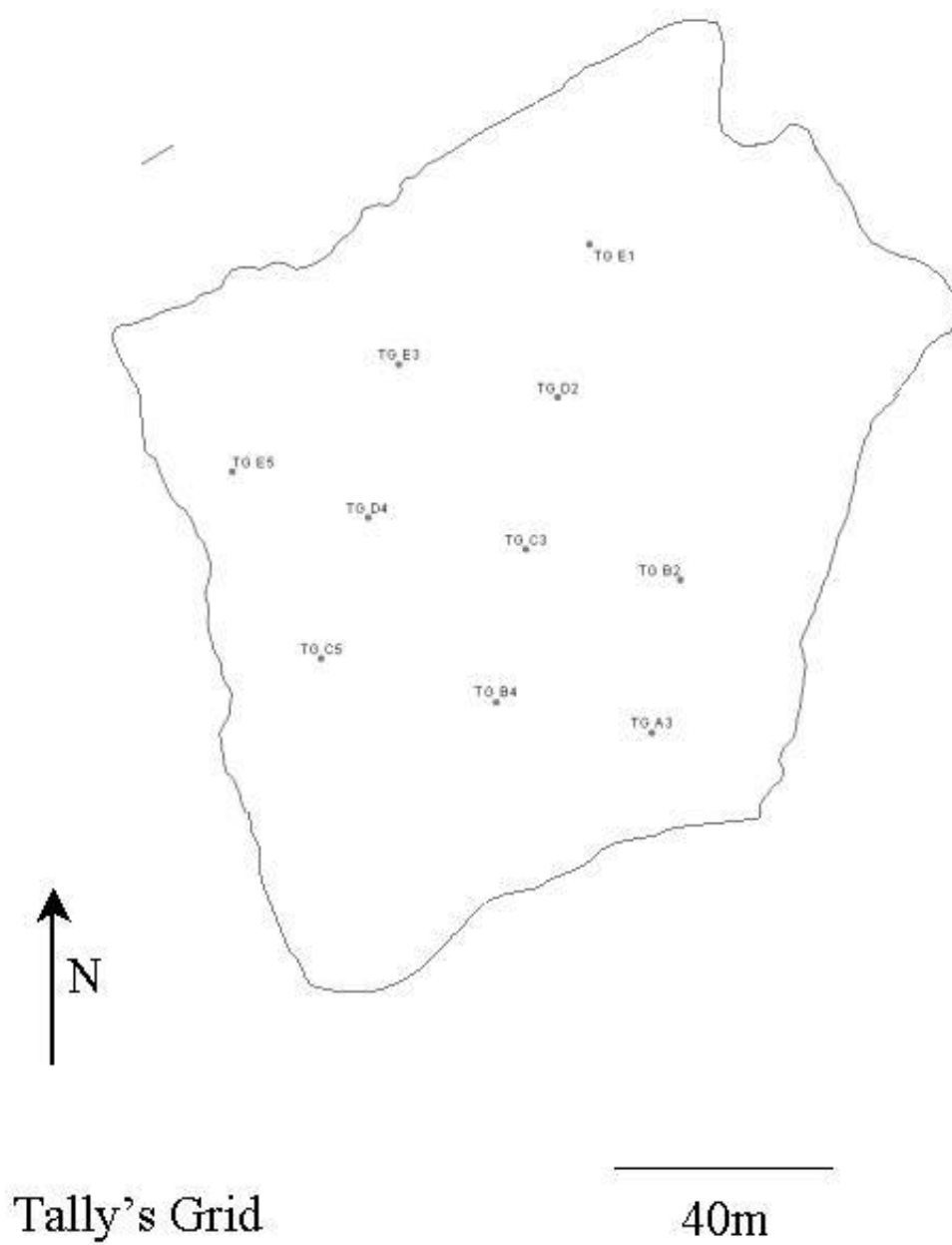


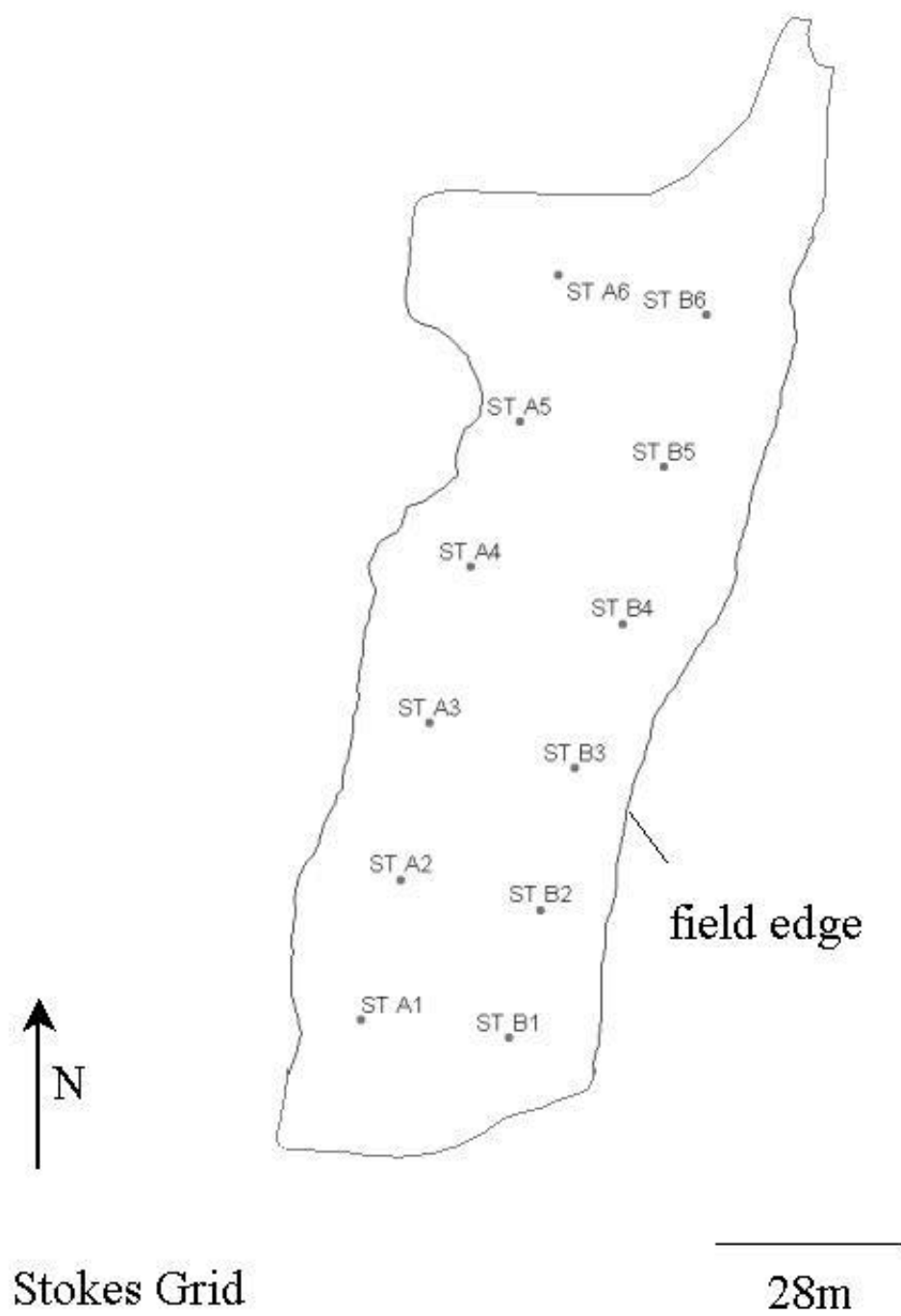
Appendix 2. Scale maps of nest-box grids used in the Tree Swallow nest-spacing study in 2001 at the Queen's University Biological Station, Ontario, Canada.

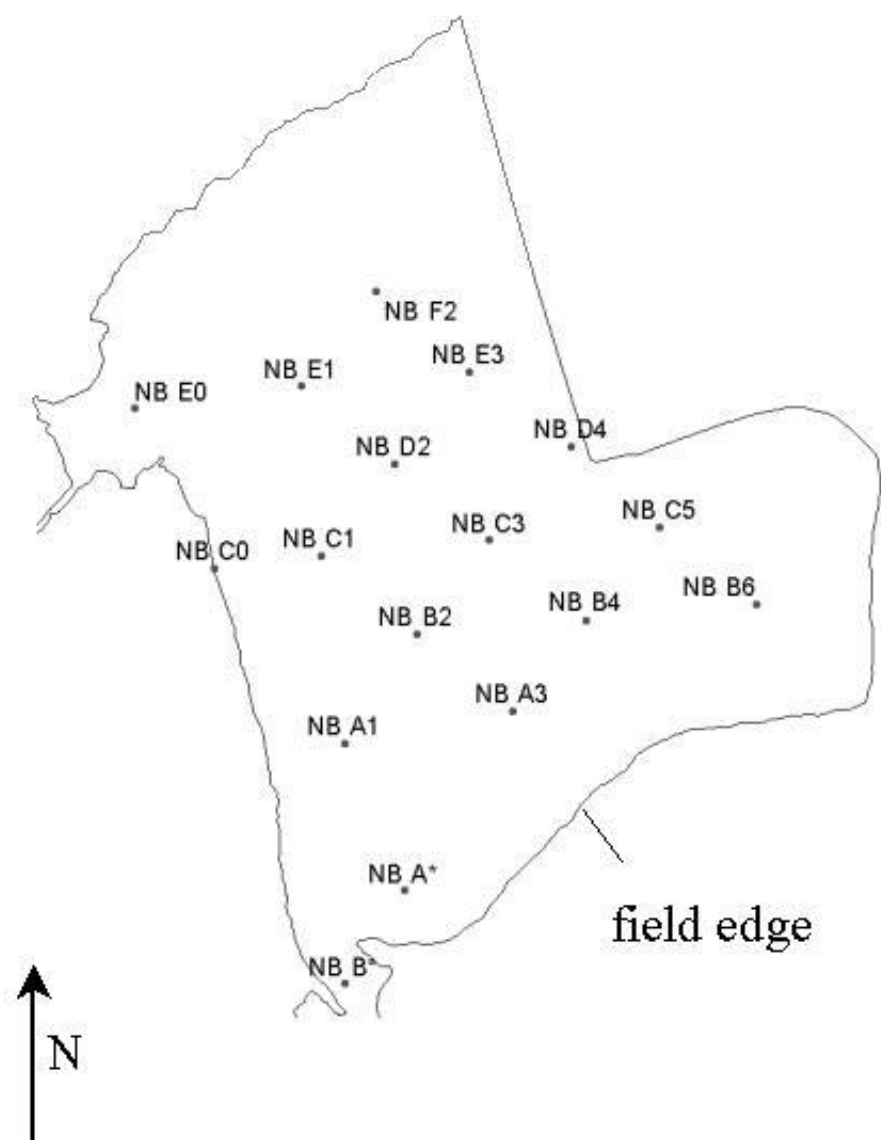


Bridget's Grid



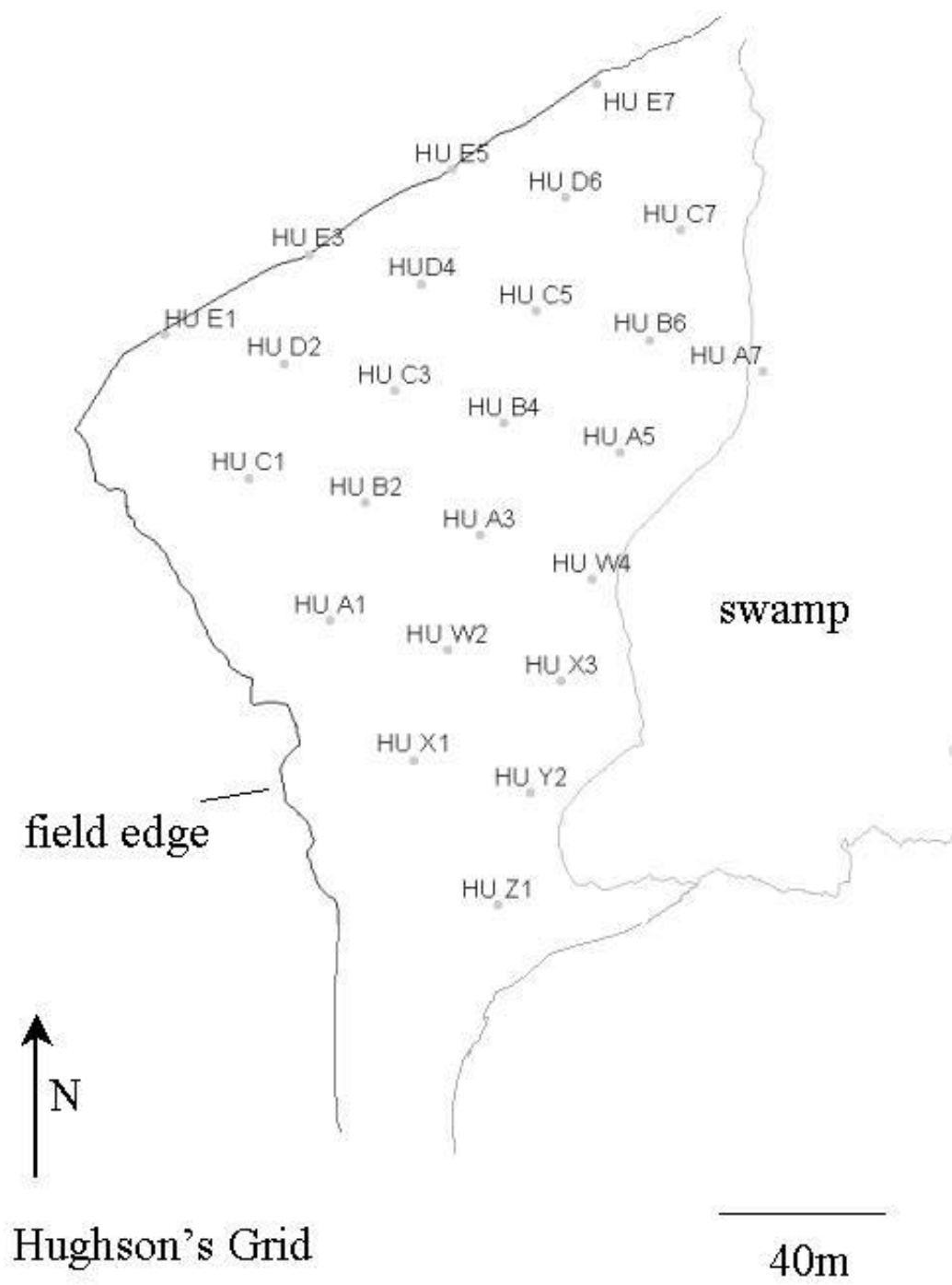


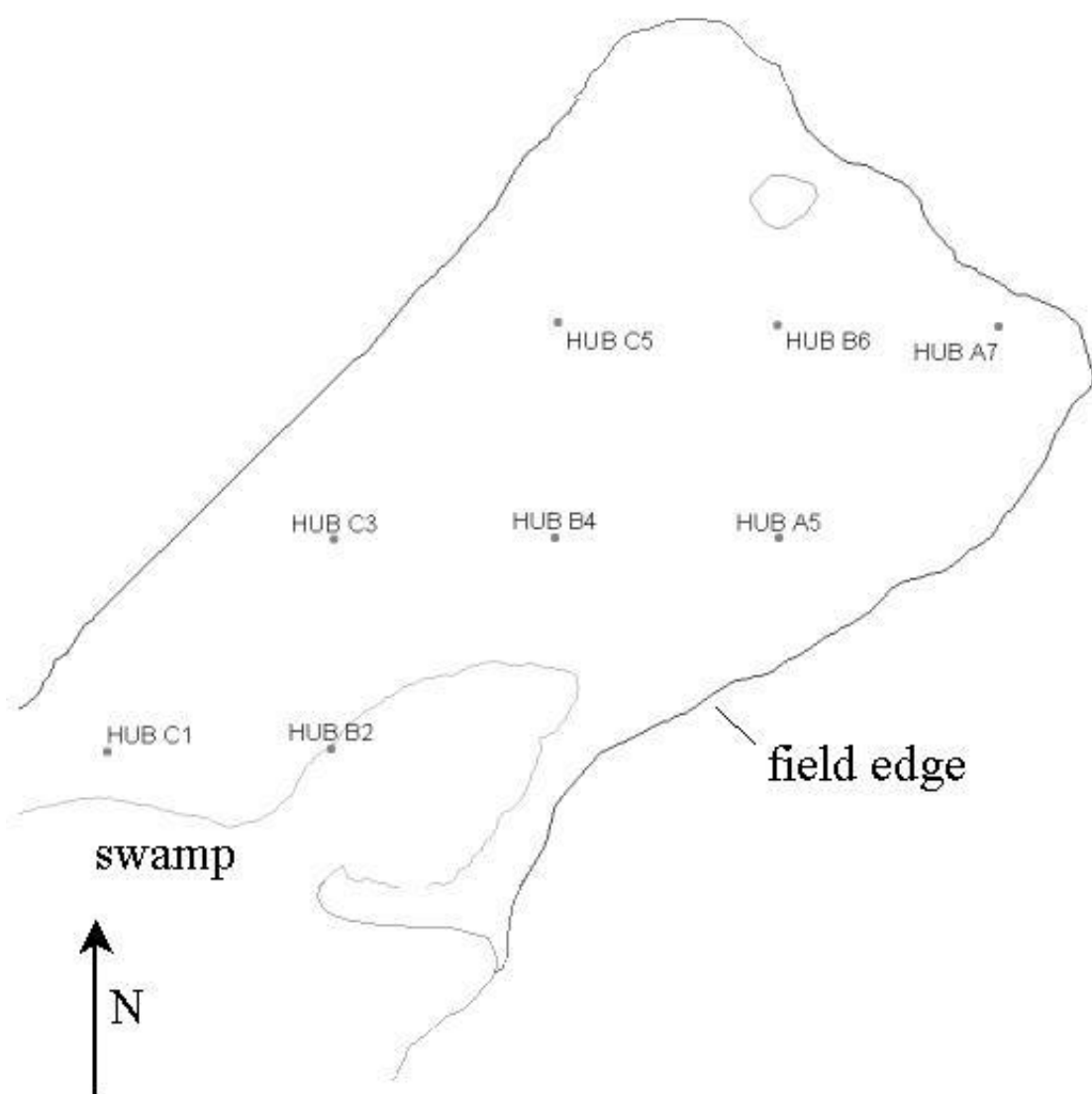




New Barn Grid

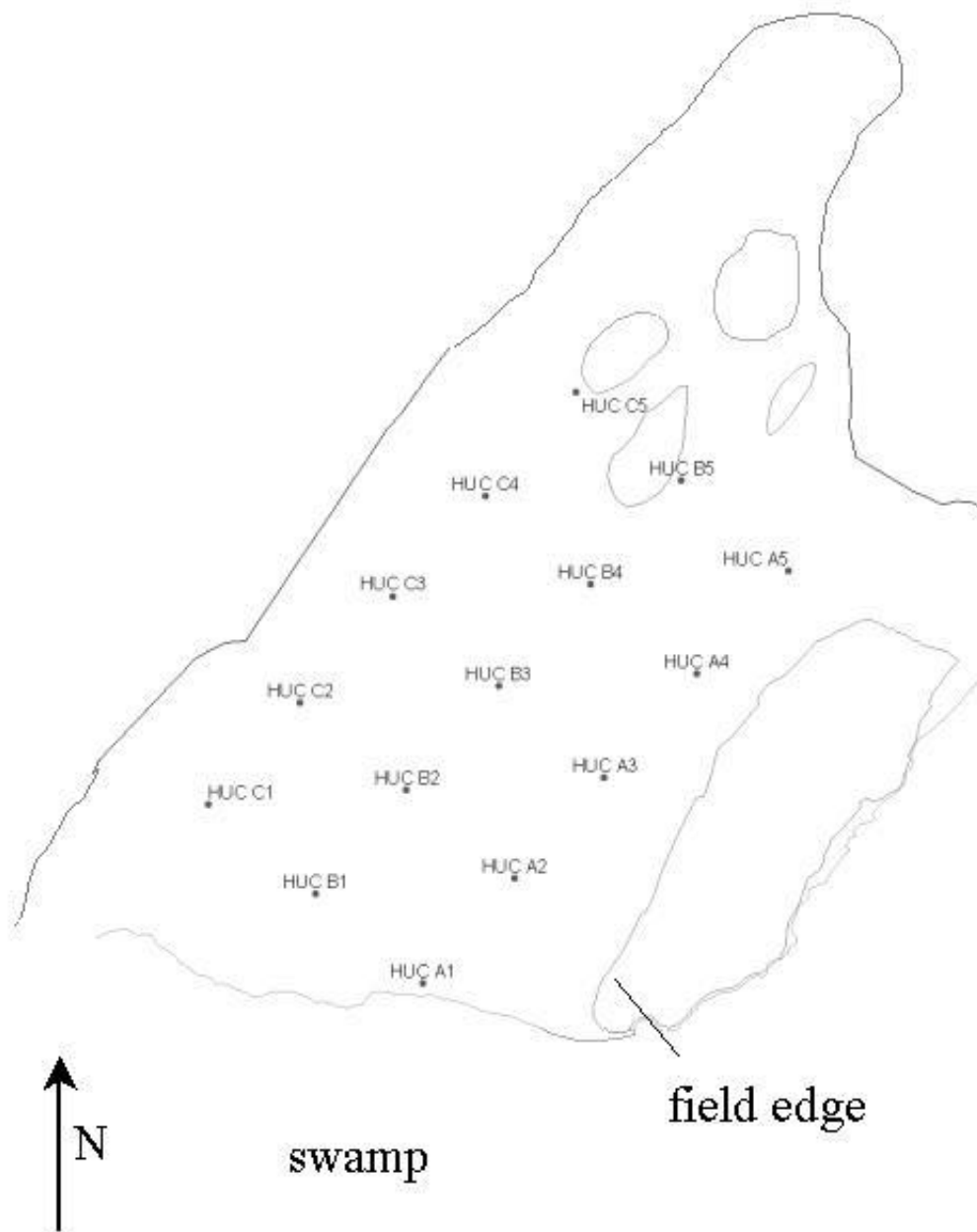
40m





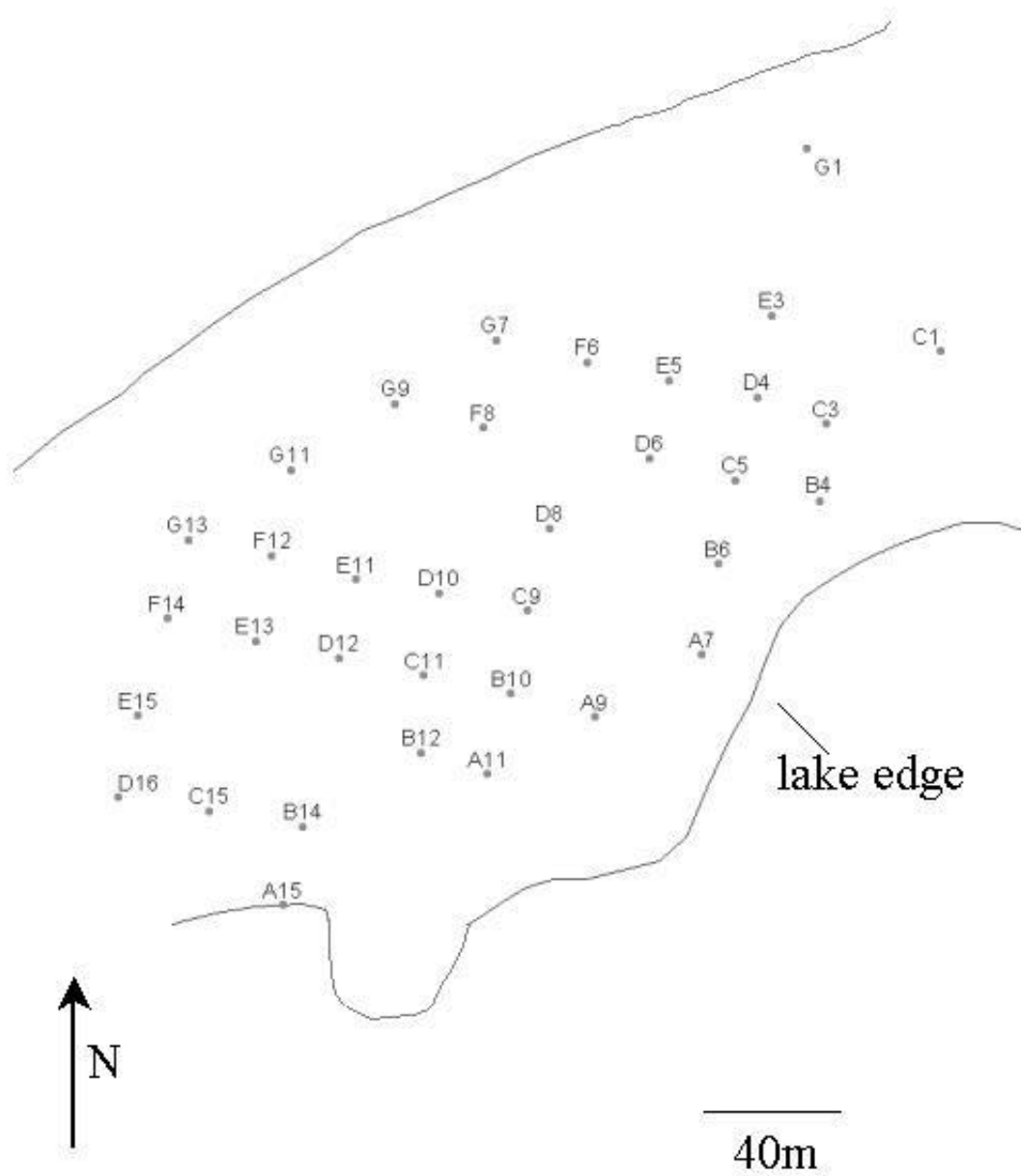
Hughson's B Grid

40m

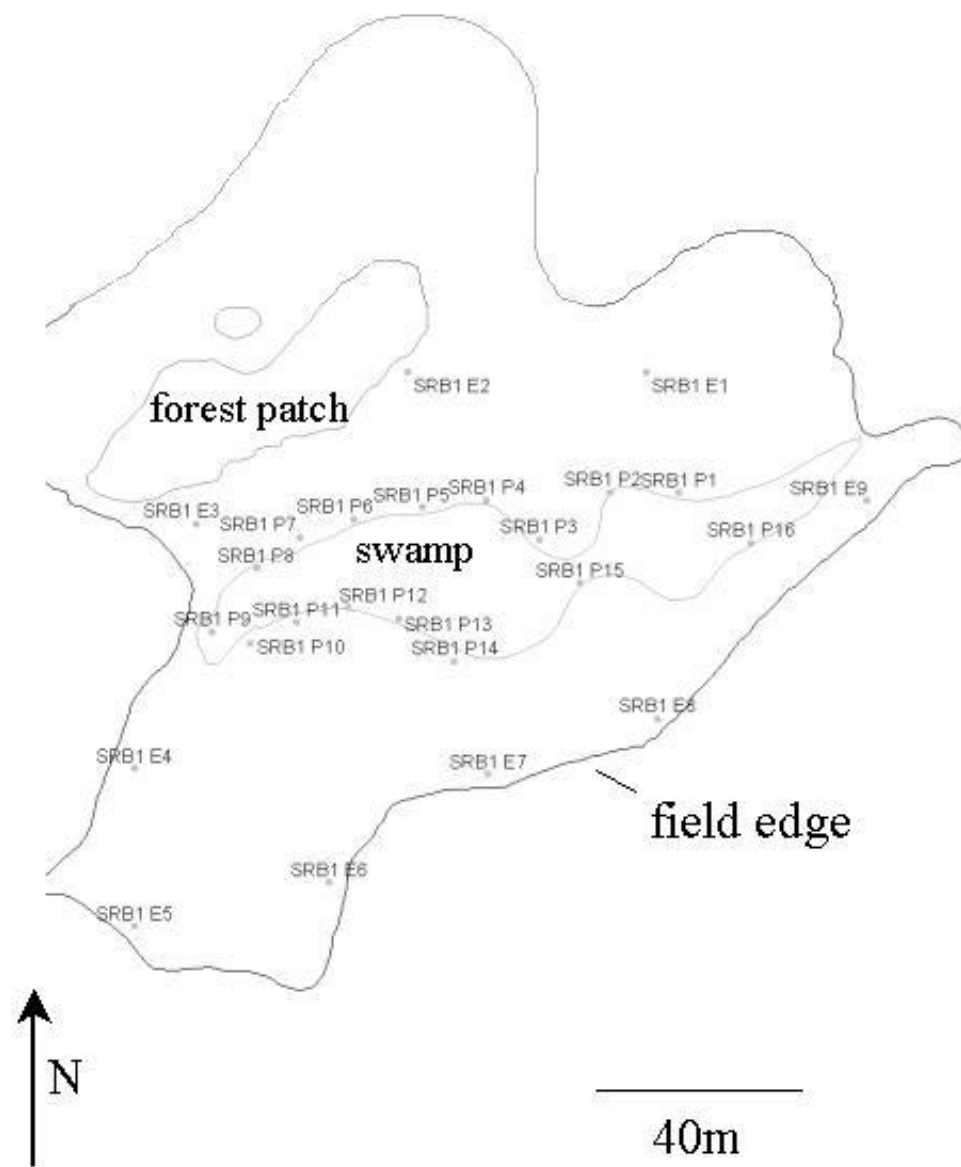


Hughson's C Grid

20m



NE Sanctuary Grid



SRB1 Grid

